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XIII. *On the Organic Tissues in the Bony Structure of the Corallidæ.**By J. S. BOWERBANK, Esq., F.G.S. Communicated by THOMAS BELL, Esq., F.R.S.*

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THE polyps of the numerous species of the Corallidæ have been known and described many years, but I am not aware that their connection with each other has been traced through the solid masses of their calcareous skeletons, or that the nature and structure of the animal tissues of these parts have, to the present period, been figured or described by any author. ELLIS, in his *History of Corallines*, published in the year 1755, has described the mode he adopted in the examination of the calcareous axes of some of the subjects of his observations, and has mentioned in several places in his work, that he had subjected them to the action of vinegar, but he does not in any instance minutely describe the results obtained by this application, nor does he describe any organic tissues or results, further than that he thus obtained the animal substance of the skeleton, freed from the calcareous matter previously combined with it. That so accurate, acute and industrious an observer, should not have seen and described more of the minute organic tissues which are now with our improved means readily to be distinguished in the tribe of animals that formed the objects of his investigations, is only to be accounted for by the want of instruments competent to observe tissues of such extreme delicacy.

My attention has been drawn to this subject from having ascertained, in one of the sponges of commerce, and in several species of sponges from Australia, the existence of a very minute and beautifully ramified vascular tissue; and in some cases of the occurrence of molecules of extreme minuteness within those vessels which appeared to me to be analogous to those of the circulation in the higher tribes of animals. These facts I had the honour of laying before the Microscopical Society of London, on the 27th of January 1841. The occurrence of such tissues in the horny skeletons of animals so low in the organic scale as the Spongiadæ, naturally suggested the idea of the probability of the occurrence of similar or more fully developed tissues in the skeletons of the higher tribes of zoophytes; and I accordingly determined to pursue the investigation, with the hope of adding, in some slight degree, to our knowledge of the organic structure of the bony portions of the Corallidæ, and also of throwing, if possible, further light upon the still contested place in the scale of created beings of the sponge tribe. With this view, I submitted small portions of nearly seventy species of bony corals to the action of dilute muriatic acid, and from thirty-five of these I have succeeded in obtaining the animal tissues in a

sufficiently perfect state to allow of a full and satisfactory view of their structure, and in many instances, the results of these examinations have been singularly interesting. I will not detail in succession the whole of these researches, but select from them such only as afford the best specimens of the tissues I am about to describe. The mode I have adopted in the examination of these specimens has been, to separate small pieces, about the quarter of an inch in diameter, from as nearly the termination of the branches or other extremities of the coral as possible, as being the most likely to have the animal tissues in their most perfect and efficient states, and to immerse these pieces in a solution of the common muriatic acid of commerce, in twelve or fifteen times its bulk of water. After the effervescence has ceased, the animal matter is usually found floating upon the surface of the fluid, in the form of an exceedingly delicate flocculent mass. This may then be removed, with as little alteration of form as possible, into some clean water in a watch-glass; a small portion, about the one-tenth of an inch in diameter, should be taken from the mass with a fine pair of scissors, and placed in a drop of water upon a slip of glass, covered with a piece of very thin glass or mica.

Upon treating in this manner some small pieces of *Millepora alcornis*, I obtained the animal matter in an exceedingly favourable state for examination. When this was viewed by transmitted light with a power of 200 linear, the mass appeared to be composed of thin glutinous animal membranes, which frequently assumed a sacculated appearance, probably caused by their having been moulded into this shape by the polyp cells of the coral. Amid this tissue there was dispersed a complex reticulated vascular tissue, floating freely between the layers of membrane, and dividing and anastomosing without any appearance of regularity. The largest of these vessels averaged $\frac{1}{5000}$ of an inch in diameter, the smaller ramifications being about half that size. Those of the greatest diameter were by no means regularly cylindrical, but threw off at short intervals numerous short cæcoid appendages, varying in length from merely tubercular projections to eight or ten times their diameters, and terminating hemispherically without any previous diminution of size. From these causes, the ends of such vessels frequently assume the ramified appearance of a Deer's horn (Plate XVI. fig. 1); other branches, instead of ending in this manner, continue dividing and subdividing until they also terminate in exceedingly minute ramifications, many of which do not exceed $\frac{1}{20,000}$ of an inch in diameter.

If we follow these vessels towards their larger extremities, we observe that they become more regularly cylindrical than that portion of them represented by figure 1, and at last they terminate in large cylindrical vessels of about $\frac{1}{3000}$ of an inch in diameter.

The smaller vessels usually enter the larger one by pairs, and a considerable increase of the diameter of the latter takes place in the immediate vicinity of the joining vessels, at the mouth of each of which there is situated a valve or diaphragm, as represented at *a, a*, fig. 2. The great vessel also has a valve at *b*, fig. 2. The course

of these large cylindrical vessels may be traced for a considerable distance, and many similar junctions of the large and small tissues be observed. They do not always join the larger so precisely opposite to each other as in the instance figured; but in all the cases observed, the valves in each of the tissues were present, although not always in the same relative position in the large vessel, being sometimes on the contrary side of the mouths of the smaller ones to that represented in the figure. Occasionally, but very rarely, a valve is to be seen in the larger vessels where no junction with the smaller ones takes place.

I have been unable to trace the large vessels to their natural terminations, but it is probable that they originate at the bases of the polyp cells, and that the valves with which they are furnished, were designed by nature to prevent the retrocession of the chyle, elaborated in the digestive organs of the polyps; and this idea is strengthened by circumstances which I shall hereafter describe.

The difference in the structure and characters of the larger and the smaller of these vascular tissues would seem to indicate that they have separate and distinct functions; in the former we observe them maintaining a uniform diameter throughout a long course without once branching or dividing, while the latter immediately decreases in size, dividing and subdividing until they terminate in vessels of extreme minuteness. The valvular structure is also a character peculiarly distinctive of the larger system; as there is not the slightest indication of such organs in the smaller vessels throughout the whole of their course, subsequent to their junction with the larger tissue. Several other corals that I examined exhibited this valvular tissue with very little variation in its character from that of *Millepora alcicornis*, but in one specimen (*Cellepora pumicosa*) it differs in so great a degree as to render a description of it necessary. Instead of being of an uniform character, and pursuing an unbroken course for a considerable length, as in *Millepora alcicornis*, it varied continually in its size, contracting in some parts to half or a third of the diameter that it exhibited at others, and especially so at the parts where the valves are situated, as represented at *a*, *b*, and *c*, fig. 3. Sometimes, as at the point *a*, fig. 4, it is terminated by an abrupt truncation and a slight lateral expansion. At each of these parts there is a valve and a new branch produced. In some cases, as at *d*, fig. 3, there is but a single branch given off with the usual valves in the branch and main trunk; and in others, as at *b*, fig. 4, there is the same form of structure observed which is so characteristic of this description of vessel in *Millepora alcicornis*. The branches given off in all the cases figured from the *Cellepora* were not belonging to the fine complex system of vessels, but of the same nature as the parent ones, giving off secondary branches, as represented at *c*, fig. 4, which have the valvular structure in every respect like the main vessel. I could not trace the connection between this valvular system of vessels and the minute contorted system with cæcoid projections, although the latter was present in abundance; but it may be fairly presumed from the result of the examination of the *Millepora*, that such a junction does take place. About the same propor-

tions are observed between the two descriptions of vessels as in the former case, but in the *Cellepora* both the tissues are much more minute than those in *Millepora alcicornis*; the average diameter of the larger vessel is $\frac{1}{5000}$ of an inch. Upon submitting some fragments of *Pavonia Boletiformis* to the action of dilute acid, and examining the animal matter thus obtained, the same description of membranous structure was observed, and a similar fine complex vascular tissue exhibiting irregularities of the structure, and in other respects so closely resembling that observed in *Millepora alcicornis* as to render a further description of it unnecessary. The larger kind of vessels were also present in about the same proportion as in *Millepora*, but they differed from them in some respects, inasmuch as towards their outer extremities they resolved themselves into a much greater number of branches, all originating at nearly the same point, as represented at *a*, fig. 5, and frequently clustered together in such a manner as closely to resemble the distorted tentacula of a dead polyp; but I do not believe that they are in reality the remains of those organs, but rather of the great ducts that have terminated at the bases of the polyps; as we find in many instances branches given off from their sides, which are surmounted by elliptical ovoid bodies, as represented in fig. 6, which have much the appearance of being incipient polyps, or gemmules which had not been projected beyond the outer surface of the coral. These bodies are divided at right angles to their axes by two or three diaphragms, and present in other respects a cellulated appearance. They occur in considerable numbers dispersed amid the tissues, and vary in size from $\frac{1}{2000}$ to $\frac{1}{500}$ of an inch in length. The branches are all of them divided at short intervals by diaphragms, so as to assume a cellulated appearance, the diaphragms becoming more distant from each other as they recede from the apex of the branch; and they are continued to some distance below the point where the branches are given off from the parent vessels, until at last they cease to appear, and the tissue assumes its usual vascular character. The average diameter of these vessels is $\frac{1}{5000}$ of an inch.

Beside the elliptical bodies, there are frequently to be seen large spherical or oval brown masses (fig. 7), whose diameter averages $\frac{1}{400}$ of an inch. They are nearly opaque, but when a bright stream of light is transmitted through their substance, they are seen to be filled with irregular cellular structure, or closely compressed granular matter. They appear always to be attached to, or to be partially imbedded in, the membrane, and are connected with each other by a beautiful moniliform tissue. When these vessels terminate at the masses, they do not abruptly enter its substance, but, dividing into minute ramifications, are spread over and lost upon its surface, as at *a*, fig. 7. In other cases they do not divide in this manner, but, preserving their integrity, they attach themselves to the surface, and, passing over a third or half of its diameter, detach themselves and resume their course, as represented at *b*, fig. 7. It is difficult to conceive the nature and purposes of these curious masses, but they bear a striking analogy to "the brown bodies" described by my

friend Dr. ARTHUR FARRE, in his paper on the Structure of the Ciliobrachiæ Polypi, in the Philosophical Transactions for 1837, p. 400, where he describes and figures them as occurring in the bases of the polyp cells. He conjectures that they are probably connected with the reproduction of the species. In many parts of the membranous structure of this coral, there appear numerous minute acicular double-pointed siliceous spicula, which do not exceed $\frac{1}{1000}$ of an inch in length, and $\frac{1}{12500}$ of an inch in diameter. They are disposed without order, and are not to be found in every part of the membrane, but only in small groups at comparatively considerable intervals. Beside these minute spicula, there are others which occur sparingly dispersed amid the tissues, and which are of a different form and of much greater dimensions. The average size is $\frac{1}{90}$ of an inch in length, and $\frac{1}{4000}$ in diameter, and they are very much in form and proportions like a common brass pin, terminating at one extremity in a point, and at the other in a spherical head, and are well represented by the spicula in fig. 8, which were found imbedded amid the tissues of a species of *Anthopora* which I shall presently describe. These larger spicula were occasionally studded with a few tubercles, and in this as in other respects were so precisely similar to the spicula of this description, which are so abundant in some species of *Halichondria* and other genera of the Spongiadæ, as to render it impossible to distinguish the one from the other, when separated from the respective bodies that have produced them. Upon examining the animal matter obtained from a species of *Anthopora*, the membranous tissue appeared as abundant as in the former cases, but somewhat denser in structure. The smaller tissue of vessels was present, although very indistinctly to be seen in parts between the membranes. The larger described vascular tissue was not detected in the portions subjected to examination. The principal features in this coral are the great abundance of large pin-shaped siliceous spicula, such as I have described as existing sparingly dispersed in the coral last referred to, and the occurrence of a profusion of the nuclei of ROBERT BROWN, or cytoblasts of SCHLEIDEN, which were dispersed over all parts of the membranous structure, as represented in fig. 8. In some parts of the tissue they were in greater abundance than in others, and especially so when a cluster or fasciculus of vessels appeared to be seated beneath them; and from this cause probably they also sometimes resolve themselves into lines, curved or straight, consisting of eight or ten cytoblasts in succession. These interesting and curious organs were found imbedded in the membranous tissues of almost every coral that I submitted to examination. In the *Anthopora* they were nearly uniform in size, and about $\frac{1}{2500}$ of an inch in diameter, but in other specimens they varied greatly in their dimensions. Their mode of disposition is also exceedingly various. Sometimes they occur singly and at long intervals; at others, as in *Anthopora*, Plate XVI. fig. 8, in great abundance, and with but faint traces of order or arrangement; while in other cases, as in *Millepora alcicornis*, they are disposed in circular groups, or in lines composed of a single series, which branch off and divide in such a manner as strongly to impress upon the mind

of the observer the idea, that this mode of disposition could have obtained only in consequence of their having been originated within the parietes of vascular tissue (Plate XVII. fig. 1). At the same time I must state, that I have examined many such branching series of these organs without being able to detect any remains of the supposed vascular tissue, which it is possible may have been absorbed after having performed the office for which it was produced; and this view of their origin is the more probable, as we observe, in many cases, the minute vascular tissue, so abundantly dispersed amid the whole of the membranous structure, frequently filled either with continuous threads of a glutinous looking matter, or of an abundance of minute detached molecules, and in one instance, represented in Plate XVII. fig. 2, I observed a series of molecules, with a few minute cytoblasts intermixed, continued beyond an irregular and indistinct termination of a vessel, no part of the parietes of which could be detected around any portion of the line of molecules and cytoblasts.

Whatever may be the origin of the cytoblasts, it is sufficiently apparent that their office is that of the production and renovation of the cellular membranous structures of the bodies in which they appear.

Upon examining the animal matter obtained from *Agaricia ampliata*, I found them developing cellular tissue upon all parts of the membrane, spreading thinly over the surface of the tissue, and, when several of them were situated together, assuming the appearance of a rude reticulated epidermal tissue.

One of the most interesting of their modes of developing tissue was seen upon examining the animal matter obtained from *Cellepora pumicosa*. The membranous tissue is exceedingly thin and even in its structure, beautifully diaphanous, and abounds in large sacculated projections (as represented in Plate XVII. fig. 3). At the termination of each of these we observe a cytoblast, which is attached to the surrounding membrane by the outer circle of its disc, from all parts of which it has projected the thin filmy tissue in a backward direction, thus producing the elongated sacculated organ upon the summit of which it is seated, and causing its apex frequently to assume a truncated or flattened appearance. The sacs may be seen in every degree of development from the cytoblast, scarcely elevated above the surface of the membrane, until they are projected to the extent of eight or ten times the amount of their own diameter. The projection of the sac is usually in the direction of a straight or slightly curved line; occasionally it forms an abrupt elbow; but in all cases the cytoblast retains its place at the extremity of the organ. Sometimes, but very rarely, there are two cytoblasts at the apex, which, having operated simultaneously, cause the organ to assume an oval instead of a cylindrical form. When the apices of two of these sacs meet, as represented at *a*, Plate XVII. fig. 3, they coalesce and appear to form a permanent union, but I have not observed that this takes place when they impinge upon any other part of the sac.

As the sac elongates, we frequently find it accompanied by minute vessels, which usually but not universally, assume a spiral direction, as seen at *b*, Plate XVII. fig. 3,

and in fig. 4. These vessels appear to be part of a system of minute vascular tissue peculiar to these organs, as they differ in character from the minute vascular tissue that we have before described as prevailing almost universally in the animal matter of the Corallidæ, being furnished with valves or diaphragms at regular intervals. But the most singular circumstance is that they appear to demonstrate the fact, that cytoblasts are not only concerned in the production of the cellular structure, but that they are also the direct originators of the vascular tissue, for in this case we observe short branches given off at nearly right angles from the minute vessels, and at the apex of each of these there is seated a small cytoblast, not exceeding $\frac{1}{7143}$ of an inch in diameter, but very considerably larger than the branch that supports it, which measured but $\frac{1}{14300}$ of an inch in diameter. Other small cytoblasts are seated upon the vessels, as shown in fig. 4, which represents one of the sacs with the accompanying vessels and cytoblasts, as seen with a microscopic power of 800 linear. The vessels are not attached to the sacs throughout the whole of their course; considerable portions of them are floating freely between the organs; and branches from these free vessels are often to be seen passing in a very singular manner half round the outer circle of the cytoblast at the apex of the sac, and, upon quitting it, proceeding to another and embracing it in a similar manner: indeed, the apices of by far the greater number of them are thus visited by branches of the vessel. It is difficult to imagine the purpose of the connection between them, but it is evident that the two organs are connected in their operations, whatever they may be.

The result of the examination of two specimens of *Nullipora* from Australia, which appeared to be of the same species, was exceedingly interesting. The cellular structure was developed in the most perfect and beautiful manner in both of them. The greater number of cells were empty, transparent, and in a slight degree larger at one end than at the other. At the smaller extremity of each there is most frequently a cytoblast, which is usually as pellucid and transparent as the walls of the cell, but in other cases it is full of a brown and indistinctly granulated matter, as represented in Plate XVII. fig. 5, which exhibits a view of the ends of the cells with the cytoblasts in this state, while fig. 6 represents a longitudinal view of the same structure in its transparent state. In this position the cytoblasts are not at all times to be seen.

In the second of the specimens examined, there was an abundance of fine membrane, with a quantity of a glutinous-looking matter adhering in irregular patches to its surface, and of the complex vascular tissue with the cœcoid appendages; thus assimilating the general character of its structure in a very close degree to that of the true Corallidæ. Although in many parts of its cellular structure it exhibits an appearance very much like that of some succulent vegetables, yet there are others in which this similarity does not obtain, and where the cells are so loosely disposed as to preserve nearly a cylindrical form (Plate XVII. fig. 7), and to assume very much the appearance of the cells of the fatty tissues in the higher class of animals: while the perfect identity of the character of the vascular tissue with that of the true corals,

combined with the glutinous animal-looking membrane, without even the slightest appearance of reticulated structures, strongly impresses the feeling upon the mind that this disputed genus is in truth animal and not vegetable, as we have been led to believe up to the present period.

An examination of our British species, *Nullipora calcarea*, assists in the confirmation of the animal view of the subject, as in this we find the cellular structure in a much less perfect and regular condition than in the Australian specimens, while the vascular tissue, with cæcoid appendages, and the membrane, are almost identical with those of the Australian *Nullipora*.

The animal matter obtained from an undescribed species of *Agaricia*, nearly allied to *Agaricia ampliata*, exhibited a form of tissue that I have not observed in any other coral. The membranous structure and the minute vessels with cæcoid appendages presented the usual characters, but the latter were not so abundant as in many of the specimens I have examined. The remarkable feature is the presence of numerous elongated vesicles, which are coated with a fine fibrous tissue regularly disposed in diagonal or waved lines across them, as represented in Plate XVII. fig. 8. Some of these organs have one or more angles in a longitudinal direction, extending from the base to the apex of the vesicle, while others have the appearance of being cylindrical sacs. They appear to be attached to the membrane throughout their whole length, as neither of their extremities is projected from the plane of the surrounding tissues. But from the different aspect of the two extremities, it is evident that they have their origin from the end and not the side of the vesicle, one termination generally being ill-defined and appearing to merge in the surrounding membrane, while the opposite one is distinctly visible. The fibrous threads of the vesicle do not pass from the one to the other, nor do they appear to originate in the membrane upon which the organ reposes.

These curious fibro-vesicular bodies resemble, in a striking manner, the fibro-cellular tissue which forms the parenchyma in the leaf of *Pleurothallis racemosa*.

I could not detect a cytoblast at either of their terminations, but a few of these organs were dispersed upon the membrane. The vessels with cæcoid appendages frequently passed over them, but in no determinate direction, and I could not detect any communication existing between them. The average size of the vesicles measured $\frac{1}{4\frac{1}{2}0}$ of an inch long, by $\frac{1}{2000}$ of an inch in diameter.

The results of the examination of the various species of *Corallidæ* which have furnished the subjects of this paper, are such as we might have expected after a careful perusal of the valuable papers of Mr. LISTER and Dr. ARTHUR FARRE, published in the Philosophical Transactions, 1834 and 1837. In the former, the author has displayed in an admirable manner the circulation of the fluids in the *Tubulariæ* and the *Sertulariæ*; while the latter, with an equal degree of talent, has rendered us familiar with the muscular organization and digestive processes of the ciliobrachiæ polypi. From these researches it is but natural we should infer that an equal extent of organ-

ization exists in the nearly allied tribe of the Corallidæ, and that from the bases of the minute polyps, the chyliferous juices should be dispersed in every direction through the common mass of the stony body of the animal, and that the usual processes of the absorption and reproduction of parts should take place within their calcareous axes, as in the corresponding parts in the higher tribes of animals.

The structures which I have described are in other respects exceedingly interesting, as they establish a degree of organic connection between the Corallidæ and the Spongiadæ, which had not, I believe, before been suspected to exist, and at the same time have a tendency to confirm the idea of the animal nature of the latter. Whatever doubts may have existed at former periods in the minds of naturalists respecting the nature of the siliceous spicula of the sponge tribe, the fact of having found these curious organs so exactly similar in every respect amid the undoubted animal secretions of the Corallidæ, will stamp them as true animal productions. The vascular tissue with cæcoid appendages has a striking resemblance to that which I have described in Part I. vol. i. of the Transactions of the Microscopical Society, as found upon the fibres of one of the species of the sponges of commerce; and in the fleshy portions of *Tethea lyncurium* and *Geodia Zetlandica*, LAMARCK, we find fleshy membranes, with minute vessels meandering through their substance in every direction, so closely resembling those obtained from the coral tribe, as to establish a degree of affinity between the Corallidæ and Spongiadæ so intimate as to appear to place the animal nature of the latter beyond a reasonable doubt. These tissues are in a like manner common to Nullipora. How far this may be the case with other apolypous corals remains yet to be proved; but should the same structures prevail in these as in that genus, it would go far to prove these curious bodies to be animals, instead of being, as heretofore considered, vegetables secreting calcareous matter in unusual quantities.

The cellular tissue of the Nulliporidæ is certainly, as regards both sponges and corals, anomalous, but the membranous and vascular tissues which accompany it are in an equal degree contrary to the types of the corresponding organs in any established vegetable body with which I am acquainted. Their true position in the scale of organization would therefore seem to be between the Corallidæ and Spongiadæ; abounding in membranous and vascular tissues, like those of the former, but totally destitute of polypiferous organisms, like the latter; while the cells and their accompanying cytoblasts are but a more methodical development of the same laws that we observed in operation in the membranous portions of almost every coral that was examined.

EXPLANATION OF THE PLATES.

PLATE XVI.

- Fig. 1. Vascular tissue with cæcoid appendages. *Millepora alcicornis*.
Fig. 2. Large vascular tissue with valves *a a* at the entrance to the vessels with cæcoid appendages, and at *b*, upon the main trunk of the vessel. *Millepora alcicornis*.
Figs. 3, 4. Large vascular tissue with valves, from *Cellepora pumicosa*.
Fig. 5. Branched and cellulated vascular tissue, from *Pavonia Boletiformis*.
Fig. 6. The same tissue with ovoid bodies at the apex.
Fig. 7. Large brown, round or oval bodies, with moniliform vessels, from *Pavonia Boletiformis*.
Fig. 8. Siliceous spicula and cytoblasts imbedded in the membranous tissue of *Anthopora*.

PLATE XVII.

- Fig. 1. Strings and groups of cytoblasts from *Millepora alcicornis*.
Fig. 2. Vessel continued by cytoblasts from *Millepora alcicornis*.
Fig. 3. Membranous sacs with cytoblasts at their apices, and minute vascular tissue with cæcoid branches terminated by cytoblasts. *Cellepora pumicosa*.
Fig. 4. One of the membranous sacs of the same, magnified 800 linear.
Fig. 5. Cellular structure in a *Nullipora* from Sydney, Australia, exhibiting the ends of the cells with the cytoblasts at the apices.
Fig. 6. A lateral view of the same tissue, with the cells empty.
Fig. 7. A single cell uncompressed, from the same, with the cytoblast at the apex.
Fig. 8. Fibro-vesicular tissue from a species of *Agaricia*, nearly allied to *A. ampliata*.
Fig. 9. Two cytoblasts from *Anthopora*, magnified 800 linear.



